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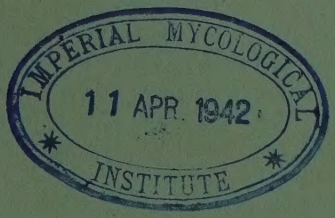

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THE BOTANICAL REVIEW

VOL. I JUNE, 1935 NO. 6

THE GYMNOSPERMS

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INTRODUCTION

During the past thirty years, researches upon Gymnosperms have dealt with morphology, taxonomy, phylogeny and, to some extent, with physiology. The fact that they are the oldest of living tree forms, going back at least to the Devonian,[1] has made the group attractive to investigators. Most of their contemporaries of the lycopod line reached their culmination, both in size and number, during the Carboniferous and, at the height of their development, became extinct. The ferns also, certainly the heterosporous[2] ones, reached their culmination at the same time, and many became extinct. However, small survivors of the lycopod line, and both large and small survivors of the fern line are abundant today. Most researches, especially those of recent years, attempt to connect the living and extinct forms. For the origin of Gymnosperms we must look to these ancient plants.

Any relationship between Gymnosperms and Angiosperms is still indefinite. Angiosperms are being found farther and farther back, certainly in the Jurassic; but they are not so old as Gymnosperms. Robert Brown's definition of Gymnosperms as seed plants with ovules not enclosed in an ovary, and of Angiosperms as those with ovules enclosed in an ovary, while it made convenient pigeonholes in the herbarium, may have hardened ideas and made it difficult to interpret forms along the border line.

The number of genera and species of Gymnosperms is still increasing, partly by discovery of new forms, especially in the southern hemisphere, and partly by splitting forms already known.

Improvements in the microscope and in technique are resulting in more detailed cytological studies; and well preserved fossil

[1] See appendix for explanatory notes.

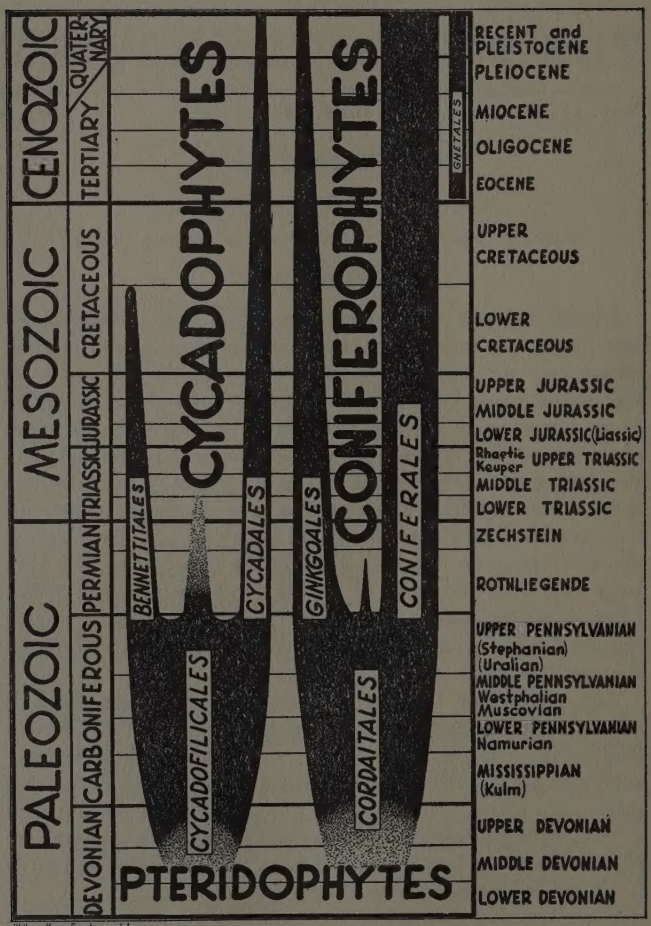

FIG. 1. Diagram indicating conjectural positions of the various gymnosperm groups in geological time. The horizons were compiled by Dr. A. C. Noé from various sources. The comparative amount of space does not equal the comparative amount of time on account of lack of space for the illustration.—From Chamberlain's Gymnosperms, The University of Chicago Press.

material, with constantly improving technique, is extending our knowledge of extinct forms. The fact that so much is being found out about fossils of the university zone of the northern hemisphere, gives hope that fossils of the southern hemisphere will fill equally great gaps in our knowledge.

The two great phyla, the Cycadophytes, comprising the Cycadofilicales, Bennettitales and Cycadales; and the Coniferophytes, comprising the Cordaitales, Ginkgoales, Coniferales and Gnetales, will be considered separately.

Cycadophytes

All three orders of this phylum have received intensive study but many problems remain to be solved.

Cycadofilicales: In England the earlier work of Williamson has been extended, principally by Scott (87, 88), Seward (90, 91), Kidston and Oliver, with younger men like Gordon, H. H., Thomas, Walton and Harris now active in research. In Europe, the most prominent names are Stur, Renault, Ettingshausen, Potonié, Zeiller, C. E. Bertrand and Paul Bertrand; more recently, Gothan, Halle, Jongmans, Kübart, Kräusel (53) and Florin (35). In America, coal-balls[3] were not known until 1922, when Noé discovered them in various places and, with his students, began a series of investigations which indicate that American material is as abundant and as well preserved as that found in England and Europe. Noé's "Carboniferous Flora of Northern Illinois" (67) shows that many genera and perhaps even species are the same as on the other side of the Atlantic.

Earlier work, which consisted largely of description of scattered fragments of stems, leaves and roots, with a smaller representation of reproductive structures, is still continuing; and occasional pieces of leaves in connection with stems, and reproductive structures in connection with leaves, are enabling workers to assemble disconnected parts of life histories. Modern technique, especially the labor saving peel,[4] makes possible rapid exploration of material. Histological details are becoming known in such a wide range of material that they serve as well as impressions in making determinations and perhaps even better in guessing at relationships.

An investigation of cuticular structures, covering both Cycadophytes and Coniferophytes, has been undertaken by Florin (35).

Both living and extinct forms are treated. The first volume, with 588 pages, 58 plates and 111 text figures has already appeared. This work is bringing to light another important feature which must be taken into account in any theories of relationship.

While the structure of stems, leaves and roots of extinct forms is becoming fairly well known and some of the vegetative features of sporangia are coming to light, little is known of the gametophytes. Since some pollen grains have been found in mature pollen chambers[5] in contact with the female gametophyte, there could have been no pollen tubes. It might be taken for granted that motile sperms of Pteridophytes were retained by early Gymnosperms.

Megaspores of heterosporous Pteridophytes have been found in such prodigious quantities that they form an important part of some varieties of coal; but megaspores still within the sporangium are comparatively rare.

In early Gymnosperms the megaspore membrane is thinner than in heterosporous ferns. Some cellular structure of the female gametophyte has been found but no well defined archegonia. The most surprising thing is that, with the great number of fairly well preserved seeds which have been sectioned, not a single embryo has yet been found. Some of the seeds, like *Trigonocarpon,* must have reached their full size, for they are several centimeters in length, the contained gametophyte seems to have reached maturity and microspores are in contact with it. These later stages are the ones usually found and they probably represent the culmination of the order. The earliest stages in transition from heterosporous Filicales to lower Gymnosperms are still to be described. Early seeds must have been very small and resemblance between ferns and early Gymnosperms almost indistinguishable in reproductive characters as well as in leaves and histological features of the stem. Dr. Fredda D. Reed (73) found in the Paleozoic lycopod *Bothrodendron* a megaspore as far advanced toward the seed condition as is the living *Selaginella apus.* With a little thicker sporangium wall and permanent retention of the already long contained megaspore, these lycopods would have attained the seed condition.

When the evidence is all in, we feel sure it must show the sequence, homosporous Pteridophyte, heterosporous Pteridophyte, seed plant.

Bennettitales: Since Wieland's (103, 107) classic work on the Bennettitales, nothing of even approximate importance has appeared. Investigators seeking material in regions where he had collected found nothing which he thought worth taking; and no new collecting grounds of equal importance have been discovered.

However, work on the Bennettitales is not yet complete. There is certainly good material of both the Williamsonia and Cycadeoidea groups in southern Mexico; and such material is in regions where living cycads are still to be found. As a promising collecting ground let us suggest the southern part of the *Dioon spinulosum* region, about 100 miles south of Vera Cruz; and the region to the west, on the other side of the mountains.

Wieland's work was devoted, chiefly, to the Cycadeoidea section of the group, the work on the Williamsonia section being largely from impressions. Both the ovulate and microsporangiate structures of the Williamsonias need much more study. The relation of the ovulate strobilus to the stem, while presumably like that in *Dioon,* is still to be determined. Gametophytes in the whole order, as in all extinct material, are still in need of accurate description. Since other structures, equally delicate, have been preserved, it must not be imagined that this part of the life history can not be found.

Cycadales: The Cycadofilicales became extinct in the early Triassic, the Bennettitales in the middle of the Cretaceous; but the Cycadales, once world-wide in their distribution, still survive in a few tropical and subtropical regions. Since they are easily recognizable in the Permian and still exist, there must have been a continuous flora throughout the Mesozoic. Occasional fossil specimens have been found, but not in abundance; and the record is almost entirely from impressions. However, their leaves and stems were so like those of the Bennettitales that many of the structures assigned to the Bennettitales may really belong to the Cycadales. Cones of the Bennettitales are mostly axillary and well protected. Consequently, they are generally preserved. Although there are some axillary cones in Cycadales, most cones are terminal and even axillary cones have little protection at maturity. Cycadales cones usually become very soft at maturity and soon decay, so that preservation in the form of petrifactions or even impressions is comparatively rare.

Studies on living forms have dealt with every phase of the life history. Chrysler (19) went to Cuba to study *Microcycas* in the field and to collect material for microscopic investigation. He found that the stem is monoxylic,[6] with distinct growth rings and that it has cone-domes[7] like those of *Dioon*. The xylem of the stem is endarch,[6] consisting typically of pitted tracheids,[8] but with a wide zone of scalariform[8] tracheids bordering on the pith. Where recognizable, the protoxylem[8] has narrow spiral[8] tracheids, followed by reticulate and then scalariform elements. In the peduncle of the male cone there is some centripetal[6] xylem, making the bundles slightly mesarch.[6] From a comprehensive study of the anatomy of the stem, leaf and peduncle, Chrysler believes that *Microcycas* is a very advanced form and not primitive as one would conclude from study of the male gametophyte.

Dr. Sister Helen Angela Dorety (26) traced the vascular system of several cycads, especially in seedlings. Her work on the seedling of *Dioon spinulosum* deals with the girdling,[9] so characteristic of cycad stems.

Dr. La Dema M. Langdon (59), also studying *Dioon spinulosum,* found the relation between leaf gaps and leaf traces[10] and showed how the girdle is built up by contributions from many leaf gaps.

Dr. Sister Mary Alice Lamb (58) investigated the leaves and leaflets of all genera and many species. They are so characteristic that she constructed a key, based upon leaflets alone. Miss Sophia Papadopoulos (68) made a comparative study of the leaves of *Ceratozamia mexicana* and *Zamia monticola* and of a hybrid between them. The cross was particularly favorable, about 50 vigorous F_1 plants having developed from the seeds. In topography and in histological characters, especially the stomata, the hybrid resembled both parents.

Dr. E. Grace Smith (96) traced the vascular connections at the apex of the stem in *Zamia floridana,* particularly in cases with numerous cones. She found stems with as many as 10 staminate cones. Usually, when there are more than two or three cones, the stem branches, so that there are only a few cones on a branch. Any cone is terminal on its own branch and brings the life of that branch to an end; but a meristem, or two meristems, may appear at the base of the peduncle and give rise to cones. Meristems may

appear in rapid succession, each one giving rise to a cone. In some cases, multiple cones are due to adventitious buds in the cortex.

One of Lawson's (60) last researches was a life history study of the Australian *Bowenia serrulata.* The prothallial[11] cell is not so persistent as in the other cycads and it does not press into the stalk cell.[11] At the first mitosis in the fertilized egg, there are two distinct spindles, one from the egg nucleus and the other from the sperm. There are only 6 free nuclear divisions in the fertilized egg before walls appear, the lowest number ever reported in a cycad and a number which is sometimes reached in the conifers.

Sedgwick (89) found that in *Encephalartos* there is a very strong prothallial cell which, with the stalk cell, presses into the body cell.[11] At the ventral canal[5] mitosis, no wall is formed between the ventral nucleus and that of the egg. The ventral canal nucleus often enlarges and fertilization of the egg by this nucleus is practically certain. Some material of *Encephalartos Altensteinii* from Fairmount Park, Philadelphia, where there was no possibility of the usual fertilization, gave strong evidence of fertilization by the ventral canal nucleus.

Dr. Dorothy G. Downie (30) visited the Pinar del Rio region of western Cuba and pollinated *Microcycas.* Plants are so widely scattered that well pollinated cones are rare. She found that the numerous sperms in this species come from repeated divisions of the so-called stalk cell, so that the stalk cell is really spermatogenous. This interpretation, which is certainly correct for *Microcycas,* suggests that the stalk cell, so generally present in Gymnosperms, may be, phylogenetically, spermatogenous, like the body cell.

Dr. Lillian Reynolds (74), studying the female gametophyte of *Microcycas,* found several groups of archegonia, on the top, on the sides and even on the bottom of the gametophyte; but only the group at the top has an archegonial jacket[5] and even this one is not highly developed. This is also the only group which has an archegonial chamber[5] and the chamber is shallow, not nearly so deep or clear-cut as in the other cycads. There are 64 or more archegonia. The number is difficult to determine on account of uncertainty in distinguishing between incipient archegonia and larger vegetative cells of the gametophyte.

Kuwada (56) investigated staining reactions of the sperm and egg of *Cycas revoluta* and, with Maeda (57), structure of the protoplasm around the blepharoplast.[11] In the same species Nakamura (66) counted chromosomes. While he found 12 in the female gametophyte and 24 in the nucellus,[5] he reports 11 in 132 cases out of 140 at metaphase of the first division in the pollen mother cell. In 8 cases the number was 12, as reported earlier by Ishikawa. Although the chromosomes are of various sizes, two gemini are noticeably larger than the rest.

In taxonomy there have been notable contributions. Pilger (71) wrote the entire Gymnosperm section of the second edition of Engler and Prantl's "Die Natürlichen Pflanzenfamilien." Schuster (85), in much greater detail, monographed the Cycadaceae for Engler's "Pflanzenreich." Schuster's strictly taxonomic section (in Latin) is preceded by sections on geographic distribution and life histories. The work brings together an immense amount of information which will be useful for reference; but it has the air of the herbarium rather than of the field. Morphologists have little interest in sub-species, varieties and forms, some of which may never occur again except that they show how much a species may vary. In this monograph, species are put together, which a field study would have separated; and species are separated which a field study would have put together. However, the work is a scholarly assembling of the morphology, geographic distribution and classification of the cycads.

Scott's (87) "Studies in Fossil Botany" has become a permanent part of the literature of Gymnosperms; and his "Extinct Plants and Problems of Evolution" (88) presents the subject in a thoroughly scientific manner and yet within the reach of those not specially trained in paleobotany.

Seward's (90) "Fossil Plants" has also become a permanent part of the literature and his "Plant Life Through the Ages" (91) traces the evolution of plants from their earliest records through the geological periods. It is intended for about the same readers as Scott's "Extinct Plants" but is more extensive and more detailed.

My own book (18), just published, has chapters dealing with field conditions, life histories and phylogeny of cycads.

Coniferophytes

The living members of the Coniferophyte phylum have received more attention than the Cycadophytes because they are dominant in the university zone of the northern hemisphere and material is easily secured. Besides, south temperate material is becoming available. The books of Scott (87, 88) and Seward (90, 91) furnish an excellent introduction to the extinct members of the line.

Cordaitales: All investigators agree that this order can be recognized with certainty in the Lower Carboniferous; but how far below that horizon or how far above, depends upon interpretations of araucoid[12] stems in the Devonian and leaves in the Triassic and Rhaetic. Kräusel (53) thinks that these lower horizon stems and higher horizon leaves cannot be assigned to the Cordaitales with any certainty; while Wieland (103–107) believes that the group goes back to the Silurian, developing into great forests in the Devonian, culminating in the Carboniferous, declining in the Permian and becoming extinct in the Triassic.

In the Devonian, practically nothing but stems is available. In nearly all cases, it seems safe to assign a piece to the Coniferophyte or Cycadophyte lines but the older the material the less marked the differences between the two lines become. Whether this means that both came from common stock or that similar conditions resulted in similar structures is still to be determined.

Florin's (35) work on cuticular structures, already referred to in connection with cycads, adds much new data which seems to be of value in determining relationships. The structure and development of stomata are illustrated and described in great detail in living Coniferales and compared with those of Cordaitales. References to his numerous papers on fossil forms are given in this book. The comparison shows definite resemblances between cuticular structures, especially stomata, of the Cordaitales and lower Coniferales, and supports the theory that the Coniferales have come from the Cordaitales or, at least, that both have come from a common stock.

Coal-balls collected by Noé in various places in Illinois are being examined and some of them contain fairly well preserved seeds of Cordaitales. There are also excellent impressions of reproductive structures (67). Dr. Fredda D. Reed has sectioned some of the seeds. They show a well preserved testa and nucellus, a strong

megaspore membrane and some cellular structure of the female gametophyte, but no archegonia or embryos. A full account will soon appear in the *Botanical Gazette.*

While stems, leaves, roots and reproductive structures have been found, leaves and stems in considerable abundance, and there has been some assembling, there is no such complete assembling of a life history as in *Lyginopteris.*

At present, it is safe to say that, so far as evolution of the vascular system is concerned, the Cordaitales have advanced further than the Cycadofilicales. Even the earliest reproductive structures of Cordaitales are cones, a stage in evolution not reached by any of the Cycadofilicales.

Ginkgoales: During the past 30 years not much has been added to our knowledge of fossil members of this order. The range has been extended and a few sections of vegetative structures have been described; but internal structure, microsporangia, megasporangia, seeds and, especially, gametophytes, still remain to be investigated.

In the second edition of Engler and Prantl's "Die Natürlichenpflanzenfamilien," Pilger (71) described *Ginkgo* and *Baiera;* and Kräusel (53) lists other extinct members. The principal investigations upon the living *Ginkgo biloba* have been by Dr. Stephanie Herzfeld (46, 47), Mann (63) and Shiamura (92).

Herzfeld, in two papers, studied field conditions, fertilization and embryogeny. It is well known that male and female strobili have been found on the same tree. Many botanists have seen the monoecious tree at Kew; but the monoecism is due to a successful graft. She mentions other grafts but thinks that the monoecious condition sometimes occurs naturally. We have never seen it and we believe that any claim must be thoroughly supported.

There are two trees in the Royal Garden at Rome which bear good seeds, although there are no male trees in the city. She also cites a tree at Germantown which bears good seeds, although the nearest male trees are six miles away. Since fertilization by the ventral canal cell is known to occur in *Picea, Pinus, Abies* and even in *Ginkgo,* it is not necessary to regard these cases as parthenogenetic.

In material collected at Vienna, she found 12 bivalent chromosomes of various sizes at the metaphase of the heterotypic mitosis

in the microspore mother cell. One of the chromosomes is definitely larger than the others and many times the size of the smaller ones. The same number was counted at the ventral canal mitosis.

The most detailed part of her work concerned fertilization and early embryogeny. At the first mitosis in the fertilized egg there are two distinct spindles, one developed from the nucleus of the sperm, the other from that of the egg. In each of the figures the x number of chromosmes was counted. Two distinct spindles were noted by Lawson (62) at the first mitosis in the fertilized egg of *Bowenia;* and, in some conifers, considerable independence of male and female chromatin has been described; but in *Ginkgo* she found the independence persisting in one nuclear generation after another, up to the seventh simultaneous free nuclear division, nearly through the entire free nuclear period, for there are only 256 free nuclei. Later, there is only one spindle and the mitoses do not seem to present anything unusual.

Six years later, Shiamura (92) studying, principally, material from the famous tree from which Hirase made the collections proving that *Ginkgo* has motile sperms, confirmed Herzfeld's count of 24 as the $2x$ number of chromosomes; but neither his description nor his numerous photomicrographs shows the paired spindles. The spindles appear broad and truncate but not double.

Mann (63) investigated reduction divisions in microspore mother cells, paying particular attention to the behavior of plastids. During prophase of heterotypic division, the plastids enlarge and some of them divide. As the telophase is reached, the plastids become arranged in two rings at the centripetal poles of the two nuclei, with approximately half of the nuclei accompanying each nucleus. At the close of the second division, the plastids are in four rings, with similar arrangement. Near the close of the second division, the outer wall pushes in between the nuclei, a process described as furrowing. When it is completed, the formation of spore coats begins. Mann believes that plastids have something to do with formation of the cell wall.

Sprecher's (98) book, dating back to 1907, is still the most complete account of the life history of *Ginkgo*.

During the past 30 years nothing has been found to weaken the theory that the Ginkgoales have come from the Cordaitales.

Coniferales: During the past 10 or 15 years, research in the Coniferales has been more persistent and widespread than in any other order of Gymnosperms. More than one-third of the papers and books listed in our bibliography deal principally or entirely with this order. There have been important contributions to all phases of life histories, comparatively inaccessible genera have been described and gaps have been filled in where accounts were fragmentary. Especially prominent among investigators who have worked on life histories are Buchholz (3–11), Hutchinson (50), Lawson (60, 61), Saxton (78–81) and Dupler (31), with text book accounts by Schnarf (82), Schürhoff (84) and myself (18). These books cover practically the entire life history and have very full bibliographies.

Covering the entire field of paleobotany are the indispensable books of Scott (87, 88) and Seward (90, 91). From the standpoint of taxonomy, Pilger's (71) revision of Coniferales for Engler and Prantl's "Die Naturlichenpflanzenfamilien" is the most important. In addition to the taxonomy, he presents a review of morphology and an extensive treatment of geographic distribution. The first volume of Florin's (35) comprehensive investigation of cuticular structures of both living and fossil forms is also of first importance.

The most recent book on paleobotany is Dr. Elise Hofmann's "Paläohistologie der Pflanze" (48). It covers the whole ground, from algae to Angiosperms, with about one-third of its 308 pages devoted to Gymnosperms and half of the Gymnosperm section devoted to conifers. It is dominantly histological; many illustrations are new. The main thesis is that plants can be identified by their histological structure. Some lower conifers, related to *Cordaites,* have histological structures similar to those of the Cycadofilicales. She believes that histological structures, especially pitting, indicate that the Araucariaceae are the oldest of the conifers, the Abietaceae coming later. In this connection it must be remembered that investigators may agree upon an evolutionary series of structures and differ as to what is the beginning and what the end of the series.

Bailey's (1) recent book deals with cultivated forms. Although the title is "The Cultivated Conifers of North America," the work will be almost equally valuable throughout the entire north tem-

perate zone. Cultivated conifers are often hard to diagnose, but with this splendidly illustrated book, determinations can be made with confidence. The author's long experience, especially with cultivated plants, has kept him from laying undue stress upon fluctuating variations which may never occur again; and his wide acquaintance with conifers in the field has enabled him to bring out differences between cultivated plants and those growing wild. Morphologists have paid considerable attention to abnormalities like bisporangiate cones and have noted them more frequently in cultivated specimens. The question might be raised whether abnormalities are really more frequent in cultivated specimens, or whether they are not merely more likely to be observed.

Pilger (71) recognizes seven families, in the following order: Taxaceae, Podocarpaceae, Araucariaceae, Cephalotaxaceae, Pinaceae, Taxodiaceae and Cupressaceae. In our own account (18) we have put the taxads and podocarps at the end of the series instead of at the beginning.

If the geological record were complete, the sequence of families would be settled by the sure testimony of history; perhaps not definitely settled, because monocots were abundant in the Carboniferous, until the "parallel" veined leaves turned out to be leaves of Cordaitales. Records in the rocks are still too fragmentary, especially in reproductive structures, to settle the arrangment.

If structure of wood be made the basis of classification, the Araucariaceae bear such close resemblance to the Cordaitales that, in many cases, determinations may not be convincing. But the Abietaceae also show some very primitive characters, perhaps antedating the Araucariaceae. If the amount of prothallial tissue in the male gametophyte be made the basis of classification, the Araucariaceae would easily stand first with Abietaceae further along and the Cupressaceae near the end. But the Cupressaceae have very primitive sperms and, some of them, numerous sperms, not far removed from the ancient swimming condition. In this feature, the Abietaceae would have a median position with the Araucariaceae still more advanced. The male strobili of taxads are of an ancient type; but the inequality of the sperms is an advanced condition and the ovulate structures, in our opinion, are near the end of an evolutionary series. If embryogeny be made the basis of classification, there would be still another sequence.

The rapidly accumulating knowledge of life histories of living forms and the gradual increase in knowledge of extinct forms is likely to determine whether the taxads should come at the beginning or the end of the series and may determine which is the more ancient, the Abietaceae or the Araucariaceae.

Of both scientific and human interest, is the work of Douglass (*27–29*) upon annual rings. He studied, principally, the rings of *Sequoia* and other conifers. The chief result was that the ring of a dry year differs from that of a wet year. A series of dry years is marked by small rings while, in wet years, the rings would be larger. By cutting a living tree and noting the sequence of rings of various sizes, a piece of timber from approximately the same locality, cut hundreds of years ago, can be dated with considerable confidence. It seems probable that the Puebla ruins of our southwest may be dated by timbers used in their construction. Of course, a piece of timber might be cut sometime before it was used but the dating would be approximately correct. Ever since Douglass made his first report in 1909, there have been accounts of rings, at first concerned more with determining the age of the large Sequoias, some of which are 4000 years old; but later, anthropologists have become much interested in this phase of botany because it seems to offer the most reliable data for determining the age of ancient buildings of cliff dwellers.

In histological structure, there is still some work on ray tracheids,[8] but they seem to be confined to the Abietaceae. Some interpret them as modified cells of the ray while others think they are modified tracheids. There have not been such detailed investigations of the anatomy of southern hemisphere forms, especially some of the more inaccessible ones, as has been given to familiar north hemisphere species.

The bars and rims of Sanio[8] have received some attention and have been found in all families of conifers except the Araucariaceae and, even here, they occur in the cone axis of *Araucaria*. Since this is a conservative region, it is assumed that the bars were formerly present in the wood. So, since they do not occur in the Cordaitales, the Cordaitales could not have been the ancestors of the Araucariaceae. While a cytological study of the origin of the vascular system of the ancestors of the conifers cannot be hoped for, such a study of living forms might help in determining their relationship to each other.

Florin's (35) extremely comprehensive study of cuticular structures, the first volume of which, dealing with Cordaitales and Coniferales, has already appeared, will at least add another character for determining relationships. The stomata and their development are treated in great detail. Ingenious technique, especially in dealing with carbonized material, has enabled him to make efficient studies of extinct forms.

Saxton (78–81), long a student of Gymnosperms, has added some later stages of the ovule of *Saxagothea* and has given the first life history account of *Austrotaxus,* an interesting new genus from the northern part of New Caledonia. The ovule is terminal and strongly resembles that of *Taxus*. Sporogenous cells are numerous and there is a tendency for more than one female gametophyte to develop, as in *Taxus*. The neck of the archegonium has as many as 16 cells in one tier. There is a ventral canal nucleus, but not a ventral canal cell. The male strobilus is very striking and, in longitudinal section, bears close resemblance to the reproductive branch of *Psilotum,* with a trilocular sporangium in the axil of each sporophyll. However, the sporangia of *Austrotaxus* are terminal, in a fused group of three, not pendulous from a peltate expansion; while in *Psilotum* the trilocular condition is believed to be due to sterilization of sporogenous tissue. Saxton objects to the term "peltate sporophyll" for either *Taxus* or *Austrotaxus* because a leaf cannot be borne in the axil of another leaf. The *Austrotaxus* cone is more primitive than the *Taxus* type and, consequently, could not be derived from it. The ventral canal nucleus divides, so that there may be as many as 7 nuclei at the top of the egg. In early embryogeny there are 8 nuclei before any walls appear and even then some of the nuclei do not divide until the next division. As differentiation proceeds, there are four tiers, an upper tier of free nuclei, a rosette of 9 cells, a suspensor of 9 cells, while the lowest tier consists of only one cell. There is no cap to be cast off later as in *Cephalotaxus*.

Saxton and Doyle (81) described the embryo and gametophyte of *Arthrotaxus selaginoides*.

Hagerup (39) secured both male and female strobili of the Sumatran *Dacrydium elatum*. In both strobili the sporangia are on the upper, adaxial face of the sporophyll, so that there is a striking resemblance to the position of sporangia in the lycopods.

He regards the strobili as inflorescences of the ament type and would apply the same interpretation to the rest of the conifers, except the Taxaceae and some of the junipers. He regards the integument of the conifers as a megasporophyll. With this interpretation, the megasporophyll (integument) of the conifers is homologous with the sporophyll of the lycopods, but not at all with the sporophyll of the Cycadophytes. Consequently, he thinks the cycads and conifers are too widely separated to be placed together in the Gymnosperms. *Juniperus,* in his opinion, stands nearest the Angiosperms.

The series of papers on *Taxus* by Dupler (31) gave a good account of the life history of this critical genus, especially of its gametophytes. The taxads are often referred to as "conifers without cones." A thorough investigation of floral development where fruiting is particularly abundant might show a female strobilus resembling a cone. If so, the present structures are very far removed from such an ancestral condition. However, it must be admitted that the male strobilus is very primitive.

A recent paper by Beal (2) deals with behavior of chromosomes at the first mitosis in the fertilized egg of *Pinus banksiana.* He finds two groups of chromosomes, as others have found them, and finds that the two spindles quickly merge into a multipolar diarch spindle with the chromosomes of the two gametes indistinguishable from each other. Each chromosome splits longitudinally and 24 chromosomes pass to each pole. He finds none of the pairing and transverse splitting described for *Abies balsamea* by Hutchinson (50). The two accounts do not agree; both may be correct but more investigation is desirable. At the present time, Haupt has an investigation of fertilization and early embryogeny in several California conifers well under way.

The most extensive work in recent years on morphology of conifers is a study by Buchholz (3–11) of the embryogeny of nearly all genera. With new and ingenious technique, he removes the embryos entire and uninjured. With such preparations, many examined in both living and fixed conditions and all of them after fixing and staining, it was easier to observe and safer to interpret, especially in the numerous cases of polyembryony. Where only one embryo comes from each of two or more fertilized eggs, the condition is called simple polyembryony. Where more than one

embryo comes from a splitting of the product of a single fertilization, the term cleavage polyembryony is used. In cleavage polyembryony (9) two types may be distinguished, determinate and indeterminate. In the indeterminate type, no embryo seems to have any advantage over the others during early embryonic competition. In the determinate type, one embryo, usually the terminal one, is more favorably situated and is usually the successful one. *Pinus, Biota, Chamaecyparis* and *Cryptomeria* have indeterminate cleavage polyembryony. *Pseudolarix* and *Dacrydium* furnish examples of the determinate type. In making such an extensive study, with as much still to be published as has already appeared, Buchholz found it desirable to make these distinctions.

As long ago as 1902, Coker noted that the terminal cell and, later, a group of cells of the early embryo, are binucleate. Buchholz found the same condition in *Dacrydium* and, in a forthcoming paper, will describe the same condition in a dozen more species of the Podocarpaceae, so that all the members of this family, except *Saxagothea* and *Microcachrys,* probably have binucleate embryonic cells.

At a somewhat later stage than that in which binucleate cells appear, an apical cell[14] was noted long ago. Buchholz has found an apical cell in *Pinus* where it cuts off segments as in Pteridophytes. He also found apical cells in *Sciadopitys, Thuja, Juniperus* and others. Forms without cleavage polyembryony, like *Picea, Larix* and *Abies,* and those with caps, like *Araucaria* and *Cephalotaxus,* have no apical cells. After a few segments have been cut off, further development is by a group of initials, a kind of transition which is well known in Pteridophytes.

Buchholz believes that polycotyledony[15] is primitive and that a lower number of cotyledons is due to fusion; while Hill and de Fraine believe that dicotyledony is primitive and that larger numbers are due to splitting.

The origin and early development of the vascular system has received little attention, because morphologists stop with the mature embryo in the seed; and anatomists do not begin until the vascular system is rather well established.

The number of families of conifers and their sequence will probably be changed many times before there is any general agreement. It seems safe to say that the order has come from the Cordaitales; what progeny it may have is still problematical.

Gnetales: The three genera of the Gnetales are so unlike that Markgraf (64) in the second edition of Engler and Prantl's "Die Natürlichenpflanzenfamilien," makes three families, Ephedraceae, Welwitschiaceae and Gnetaceae.

The most extensive investigation of recent years and the one containing the most original work is the posthumous book, "Gnetales," by Pearson (69). The book was well under way when he died in 1916. Professor A. C. Seward, with the cooperation of Mrs. Thoday, completed the work, with the aid of Prof. Pearson's notes, and the book was printed in 1929. It covers geographic distribution, taxonomy, life histories and relationships.

Herzfeld (46, 47) made a detailed investigation of fertilization and nearly related stages in *Ephedra.* She described fertilization of the ventral canal cell by one of the sperm nuclei and fertilization of the egg by the other. The product of the fertilization was two groups of free nuclei. She did not hesitate to regard this as double fertilization in the Angiosperm sense.

A thorough investigation of *Ephedra* by Dr. S. Flowers with an abundance of well fixed material is now well advanced. This work will supplement the classical study by Land.

The origin of the Gnetales is still obscure. No reliable fossils have been found below the Tertiary and it is just as indefinite whether they have any progeny. *Ephedra* has unmistakable Gymnosperm characters and the other two genera resemble *Ephedra* in many ways, so that the three appear to belong together.

In the evolution of the vascular system, all three are very advanced, with vessels in the secondary wood, and *Gnetum* may have companion cells[13] in the phloem. The floral diagram of the male flower of *Welwitschia* bears striking resemblance to that of a tetracyclic Angiosperm flower and has led some to claim that the Gnetales are the ancestors of the Angiosperms. The evolution of the gametophyte, especially of the female gametophyte, is very advanced, with *Gnetum* almost in the Angiosperm condition. In general habit, *Gnetum,* with its netted veined leaves, would be mistaken for a dicot by any one except a botanist. But the fact that there are resemblances to Angiosperms does not prove that the Gnetales are becoming Angiosperms or that they have given rise to any Angiosperms. It can only be claimed that, developing along fundamental lines of evolution, they have advanced almost

as far as the Angiosperms. Even the most primitive forms are so advanced that they must have had a much more remote ancestry than has yet been discovered.

Phylogeny: Morphology, physiology and genetic relationship should precede taxonomy if taxonomy is to be anything more than a series of artificial keys for finding out the names of plants.

Similar structures are still the basis of all schemes of classification, but in phylogeny similar conditions may be responsible for many similar structures. Vegetative structures most intimately concerned in the life of the plant are likely to be the first to respond to changing conditions. Leaves are particularly responsive. Stems might be mentioned next. Gametophytes and early embryogeny may be the most stable features because they are less exposed to the struggle for existence. The embryo of *Lilium,* in all parts of the world, in warm or cold regions, in wet or dry conditions, is developed from four megaspores not separated by walls; while the stems, leaves and flowers show great diversity. The plant bodies of some euphorbias and some cacti are very similar, although there is no genetic relationship.

It is devoutly to be wished that more and better material of Paleozoic and Mesozoic forms be studied, especially gametophytes and embryogeny. Some vegetative material is so well preserved that one can reasonably hope that equally well preserved material of reproductive structures may yet be found. When records have become much more complete, such problems as comparative antiquity and origin of Araucariaceae and Abietaceae may be settled definitely; and we shall know whether to begin treatment of conifers with taxads or pines. Just now, from study of the literature, especially that of the past twenty years, there seem to be two strong lines, the Cycadophytes and Coniferophytes, both already highly developed in the Permian and differing so much from each other that they may not have had a common origin. From the Cycadofilicales, the Bennettitales and Cycadales have arisen independently. The Cycadales did not come from the Bennettitales. The Cordaitales, in our opinion, gave rise to the Ginkgoales and Coniferales. The Gnetales must have a more extended geological history than has yet been discovered; but at present, they seem to be a group with neither any yet discovered ancestry or progeny.

APPENDIX

By the Editors

Readers especially interested in the Morphology of Gymnosperms are urged to consult Prof. Chamberlain's latest revision of his classic study upon the subject (citation No. 18). For those to whom this volume may not yet be available the following notes are here appended. They are presented only to furnish a general background for the accompanying article which discusses the entire group and necessarily involves terminology partly peculiar to the subject.

1. See fig. 1. for succession of geological eras.

2. *Heterospory,* the possession of two different kinds of spores, micro- and megaspores, is characteristic today of all seed plants, of the Water Ferns and of a few lycopods or club-mosses. It represents an evolutionary advance over homospory.

3. *Coal-balls* are calcareous nodules containing petrified patches of vegetable debris from the marshes and swamps of the closing stages of the Carboniferous period (Seward).

4. The *peel method* involves etching of a flat surface of material with acid and then flooding the surface with celloidin. The latter is subsequently peeled off, carrying remarkable detail of the embedded fossil.

5. The *megaspore* is the first cell of the female gametophyte. It is a cell of the nucellus of the ovule and is immediately surrounded by vegetative cells of the *nucellus.* It enlarges at the expense of these surrounding tissues and by successive nuclear divisions acquires many free nuclei, hundreds in some cases, which surround a large central vacuole. Wall formation then ensues about these nuclei and further centripetal development of tissue finally fills the entire original and now enlarged megaspore. The tissue, thus developed, constitutes the *endosperm* which, in this case, is the *female gametophyte.* At varying times during formation of this tissue certain superficial cells at the micropylar end, many in some cases, become *archegonial initials.* Except in *Welwitschia* and *Gnetum* each such initial enlarges and divides into an outer *primary neck cell* and an inner *central cell.* The former divides once in the cycads and *Ginkgo* producing two *neck cells;* in conifers the number is variable. The central cell then enlarges considerably and the surrounding layer of endosperm cells becomes differentiated as the *archegonial jacket* and performs some nutritive function for the contained *egg cell.* The nucleus of the enlarged central cell divides at a certain time to form the *ventral canal nucleus* and the *egg nucleus.* Adjacent cells of the endosperm may grow faster than the neck cells, pushing out the nucellus and forming a funnel-shaped *archegonial chamber* with the neck cells at its apex. This chamber is separated by the nucellus from the *pollen chamber* into which microspores enter through the *micropyle* or opening in the integuments which enclose all these structures. Microspores germinate in the pollen chamber, their tubes penetrate the nucellus and enter the archegonial chamber where they discharge swimming sperms among cycads and *Ginkgo* while in conifers they penetrate into the egg cell without formation of motile sperms.

6. Xylem is said to be *endarch, mesarch* or *exarch,* terms which refer to the radial direction of maturation of vascular cells with respect to the center of the axis, not to the center of the vascular bundle. If this progressive maturation, leading to differentiation of so-called *protoxylem* and subsequently to *metaxylem,* progresses away from the center of the axis toward the outside, growth is said to be *centrifugal* and the xylem is *endarch.* This condition prevails in stems of seed plants. If direction of maturation be toward the center of the axis, growth is *centripetal* and the xylem is *exarch.* This is true of all roots and of the axis of club-mosses; it is regarded as primitive. The intermediate condition, where maturation progresses both centripetally and centrifugally, is common in ferns and the xylem is then *mesarch.* If only one vascular cylinder differentiates from meristematic cells at the stem apex the stem is *monoxylic.*

7. *Cone-domes* appear in the pith and are groups of vascular bundles from the apex of which peduncles of cones arise. In longitudinal sections of the stem the bundles appear to form a convex diaphragm across the pith and in transverse sections as a circle of vascular bundles.

8. *Protoxylem* refers to the first cells to mature in the development of a vascular strand. The component tracheids have only *spiral thickening* which permits elongation; when thickening becomes *reticulate* or *scalariform,* in later maturing cells, further elongation is no longer possible. *Pitted tracheids* are the narrow, elongated, dead cells of xylem whose walls are thickened except for tiny, circular pitted areas. In most conifers special thickenings, known as *bars* or *rims of Sanio,* are located between pits on lateral walls of tracheids. In scalariform tracheids these thickened areas are narrowly elongated at right angles to the long axis of the cells. While tracheids are almost exclusively perpendicularly arranged in stems, in certain species some are horizontal, constituting part of the wood rays, and are then known as *ray tracheids.*

9. *Girdling* refers to the peculiar course of bundles which enter leaves of cycads. They join the vascular system of the stem, not near the base of the leaf but elsewhere, sometimes on the opposite side of the stem.

10. *Leaf gaps* are areas within the stems of ferns, gymnosperms and angiosperms where cortex and pith are continuous. They represent interruptions in the vascular cylinder where cells did not mature into vascular elements. They are located around and above the point of departure of *leaf traces.* The latter are prolongations of the vascular system of the stem into the leaves.

11. The uninucleate pollen-grain or *microspore* is the first cell in the *male gametophyte.* By successive divisions of the original nucleus a variable number of walled cells is formed within the microspore wall before the latter is shed from the microsporangium or pollen sac. In cycads the pollen is shed in a three-celled condition, one of the cells, the *prothallial cell,* being smaller than the others and representing the vestige of the prothallium in lower plants. This prothallial cell persists. In *Ginkgo* two such prothallial vegetative cells form, one of which disintegrates and the other persists as the single cell does in the cycads. In certain conifers

two such vegetative cells also appear in the microspore but both disintegrate. These stages represent evolutionary steps in decrease of vegetative tissue in the male gametophyte.

Another of the three cells in the cycad pollen, formed previous to shedding, is also small and known as the *generative cell.* After pollination and germination of the microspore within the *pollen chamber* of the ovule, this *generative cell* divides to form the *stalk* and *body cells.* The former of these is regarded as representing the stalk cell of an antheridium and the persistent prothallial cell in most cases presses into it. The *body cell* is the real spermatogenous cell. At a certain period a small structure known as the *blepharoplast* appears in it. The body cell later divides, along with the blepharoplast, into two sperm mother cells. Each of the latter produces a sperm with a spiral band of cilia developed from a blepharoplast. These motile sperms are the largest known among plants or animals.

Approximately the same sequence of events occurs in *Ginkgo* including the blepharoplasts and motile sperms. Body and stalk cells form from the generative cell also in conifers but blepharoplasts do not develop in the body cell and motile sperms do not form. The body cell divides directly, on the contrary, into two non-motile male cells (or only nuclei). A cell generation is thus significantly omitted, namely, the sperm mother cells of the cycads and *Ginkgo.*

12. Resembling *Araucaria,* a genus of conifers found now only in the southern hemisphere.

13. Except in the Gnetales, gymnosperm wood differs from that of angiosperms, among other features, in not having *vessels.* The latter are dead cells, usually wider than tracheids, which are joined together into tubes by disappearance of their end walls. *Companion cells* of angiosperms accompany conducting *sieve tubes* in the phloem and their nuclei are thought to serve the apparently enucleated sieve tubes.

14. Growing points of seed plants consist of many dividing cells. In ferns, on the other hand, all cells in these regions can be traced back to one *apical cell.*

15. Cycads and *Ginkgo* usually have only two cotyledons or seed-leaves per embryo. Conifers have a greater and variable number referred to as polycotyledony.

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THE PRESENT STATUS OF THE PLANT ASSOCIATION

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Editorial preface

The plant association has often been compared to the species. One point of agreement between them is that both have been subjects of strenuous discussion concerning their definition and scope. The species-question has been before us for more than a century, but has never been settled. Opinions still vary from the micro-species, consisting possibly of a single pure-line race, to the broad or Linnaean concept. The prevailing taxonomic usage of the term has been a matter of long development and is in general fairly well understood.

The association-question, on the other hand, was only recently thrust upon ecologists. They have attempted energetically to settle the various problems involved in it, generally by the advancement of individual opinions rather than by the slower method of gradual development through long experience.

The fact that definite societies or assemblages of plants exist in nature is an accepted fact. The proper interpretation of these societies, the terminology to designate them, and the general principles of their classification into larger vegetational groups are still matters of controversy.

What is a plant society? What is the underlying basis for its existence? Is it a concrete thing or an abstract concept? What is the fundamental unit of vegetation, corresponding to the species in taxonomy? Is it broad or narrow in its scope and by what name shall we call it? Can we group plant societies into larger complexes and can we logically recognize minor subdivisions of them?

Some of these questions are discussed by Dr. Pavillard in the present paper. The editors regret that it has been impossible to maintain the sparkling vivacity of the original French.—H. A. G.

The association as the fundamental unit in plant sociology

In the section of Phytogeography of the International Botanical Congress at Brussels in 1910, a serious attempt was made to reach

an international understanding on the concept of the plant association. The definition proposed by Flahault and Schröter deserves to be restated: *An association is a plant community of definite floristic composition, presenting a uniform physiognomy, and growing in uniform habitat conditions. The association is the fundamental unit of synecology.*

It is obvious that this statement consists of two parts. The first one has the character of a definition; it was not adopted by the Congress. The second has a systematic significance and assigns to the association a certain hierarchal rank and value; it was not particularly discussed at the meeting of May 20, 1910.

Now the importance of the first part of the statement clearly depends on the second, since in every experimental science the existence of a fundamental unit is the prime requisite for precision and exactness in the comparison and subordination of the subjects studied. If we admit that the association has this rôle of a fundamental unit, then we must also conclude that its most important characters are those which are most directly related to this rôle.

The oldest definition which reflects the importance of these characters was propounded by Du Rietz and his colleagues in 1920: An association is a plant society with definite constants[1] and definite physiognomy (22).

In this definition, the essential criterion and the only one which has been the subject of detailed study is the presence of a determinable number of constants. This number may be ascertained by the statistical application of the quadrat method,[2] and depends on the determination of the *minimum area,* which is the smallest extent of space which can be characteristic of each association.[3] In the minds of the Swedish authors, then, the recognition and delimitation of associations was a matter of rigorously precise procedure, which is alone capable of assuring the validity and comparability of groups worthy of being regarded as authentic associa-

[1] A constant is a species which is regularly present in every example of a plant association.—Editor.

[2] A quadrat is a small area of definite size, often one square meter, within which vegetation may be studied intensively. Results obtained from a sufficient number of quadrats yield important averages and may be used in statistical studies.—Editor.

[3] That is, it will contain the typical species and a fair representation of the others of secondary importance, and will in general be a fair sample of the whole association.—Editor.

tions. We shall refer later to the present fate of this method of work, so imperiously promulgated by Du Rietz in 1921 (14).

The practical result of the initiative of the Upsala group was to induce a certain number of Nordic ecologists and a few others to pulverize the vegetation of their respective countries into an innumerable multitude of minute rudimentary groups, under the name of associations, generally covering a very restricted area and corresponding accordingly to the lowest rank in the phytosociological hierarchy.

The publication of Du Rietz' voluminous dissertation opened an era of ardent polemics which are of no interest today. However, the arguments developed by Rübel in his philosophical essay of 1925 (62) merit brief consideration because of their ingenuity and their results. Attention would have been awakened differently in Sweden and in Switzerland by certain forms which are particularly frequent in the vegetation, said Rübel, and there would have resulted in the two countries a different concept of the association and a different technique. Study of the heaths covered by dwarf shrubs in Sweden would have led to micro-associations; study of the meadows of Switzerland would have favored macro-associations. There would thus have developed two parallel and possibly equally legitimate systems. Is it possible to unite them into a single system, or in other words to coördinate and subordinate the two kinds of associations, the small and the large?

Pursuing his efforts for conciliation and seeking to introduce new aspects into the argument, Rübel (63) returned to the question in 1927. Without ceasing to champion the classical partition of the association into sub-associations and facies characterized by differences in floristic composition, he considers the advisability of borrowing from the British and American ecologists another sort of subdivision based on physiognomic dominance.[4] Two new ranks, the *consociation* (12) and the sociation,[5] may thus be subordinated to the association, which still always maintains its dignity as the fundamental unit.

It is impossible not to recognize the effect of these suggestions by Rübel upon the new attitude adopted by Du Rietz in 1930, just

[4] See footnote on page 225.

[5] The term *society*, familiar to English-speaking ecologists since its presentation to the Brussels Congress by Tansley and Moss, is thus converted (fortunately?) by Rübel into *sociation*. Gams (25) gives the name society

before the Botanical Congress at Cambridge. His voluminous memoir in Abderhalden's Handbook (18) includes a reform project still more radical and extraordinary than his "laws" of 1920. Appropriating the terms consociation and sociation, Du Rietz incorporates them as inferior steps into an entirely new hierarchy for which he is alone responsible, although he seems erroneously to attribute the preliminary proposal of his innovations to Rübel.

The association still appears as the third stage[6] in his classification, but is now completely deprived of its systematic importance in favor of the sociation, which, according to Du Rietz, is the sole fundamental unit, alone analogous to the species, alone perfectly homogeneous and truly natural in all its parts. It is needless to say that such a concept could not be accepted by the majority of ecologists of central Europe.

At this time we shall not discuss or pass judgment on Du Rietz' system as a whole or on his terminology. The chief interest of his project, from our special point of view, lies in the definitions of the Swedish author and especially in that of the sociation, his fundamental unit, which is to be characterized by the presence of *constant dominants* in each stratum (layer) of the group.

In 1920 the association of Upsala, the exact equivalent of the sociation of 1930, was to be recognized, according to Du Rietz, chiefly by its *dominant constants*. Today we read *constant dominants*. Although this appears to be a simple inversion in the position and meaning of the words, it is not without its significance, and is in fact evidence of a complete and entirely unexpected reversal in the doctrine and ecological technique of Du Rietz.

Let us briefly recall what this technique was, according to his memoir of 1921: first, preliminary reconnaissance in the field of the probable associations according to the dominant constants; next, the necessary confirmation of this observation by determining the group of constants and the corresponding minimum area by the statistics of the quadrat method. That is the only method, said Du Rietz, through which definite and unimpeachable conclu-

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to aggregations of individuals of a single species or several species belonging to the same life-form. As the "fundamental unit of vegetation" the society must, according to Gams, be translated by *Bestand* as its equivalent term in German and Scandinavian.

[6] Ranking above the sociation and consociation.—Editor.

sions may be reached. How many times has Du Rietz claimed not only the superiority but the indispensability of his technique?

Of this Upsala method, so rigorous and precise, at least in appearance, nothing now remains. Not only does Du Rietz completely abandon his laws of constancy and his earlier definitions, but he now bases his diagnosis of the sociation on the dominants alone, asking for nothing else except a purely empirical floristic list as a source of supplementary information.[7]

The present purely empirical method of determining sociations justifies us in considering them as absolutely incapable of filling the rôle of fundamental units.

Du Rietz seems to have realized the serious inconvenience of the strange, almost paradoxical situation in which he placed himself. Less than two years after the Congress at Cambridge he discarded completely, although reserving for the future, most of his creations of 1930, especially the long series of synusia, which interest scarcely anyone. For the same reason he has also given up the attempt to secure official consecration[8] of his minor floristic units, the sociation and the consociation. For the Congress of 1935 he merely proposes a very limited program, the essential features of which concern the formation and the association. One can almost believe that he has gone back twenty-five years to the eve of the Congress at Brussels.

This is not the place to discuss the formation, which is not a part of our present subject.

In regard to the association, Du Rietz restricts himself to the proposal that a uniform use of the term should be agreed upon, applying it, if possible, to an ecological group of about the same rank as the associations of Braun-Blanquet and his followers. We are naturally quite disposed to rally round these propositions, but on one condition, which Du Rietz does not mention and which in our opinion should prevail above all others, and that is that

[7] What a curious spectacle is presented by some of these changes of attitude. After being converted to the technique of the Upsala school and having introduced it into Russia (36), and after earning the praises of Du Rietz (17), N. Katz (35) today places the statistical problems of the Scandinavian investigators and the so-called laws of constancy among the "ballast-problems . . . . . which do not repay the time and trouble devoted to them." According to Katz, the term association and its use as a fundamental unit should be applied only to groups of restricted extent, corresponding to the sociations of Du Rietz.

[8] I.e., adoption by a botanical congress.—Editor.

the association thus conceived should be capable of acceptance and recognition by all as the fundamental unit of plant sociology.

The concept of the association

What is meant by the term association? An important question, and an essential one for all who consider the association as the fundamental unit of plant sociology. Two conflicting theses, equally interesting, have been supported by A. G. Tansley and by H. A. Gleason.

Tansley (69) adopts from Clements the principal of the organic individuality of groups and develops extensive analogies between groups and living individuals; incidentally also between plant and human societies.[9]

In admitting "that vegetation forms natural units which have an individuality of their own," Tansley places himself among those investigators who have to "focus their attention on the vegetational units themselves." Now "the treatment of vegetation as consisting of natural units * * * seems to involve their consideration as organic entities." "These units owe their existence to the interaction of individual plants of different species with their environment" and with one another (Cf. Yapp, 77). Undoubtedly "these natural entities * * * are not organisms, in the full sense in which we apply the term to an individual animal or plant." But "it is clear that the aggregation of plant individuals which we call units of vegetation or plant communities have some of the characters which we associate with organisms."

An analysis of the general character of human societies leads Tansley to create for them the concept of "quasi-organisms." A comparative examination of vegetational groups permits him to conclude that "though less like true organisms than human communities, plant communities may still be regarded as quasi-organisms or organic entities, for on the one hand they are composed of organic units and, on the other, they are certainly entities, in the sense that they behave in many respects as wholes and therefore have to be studied as wholes."

This being admitted, "we must recognize * * * that not all plant communities are of equivalent value. * * * The organizing factors of vegetation * * give rise to various grades and kinds of aggre-

[9] Compare Harper (33).

gates. * * The general recognition of the association as the fundamental unit of vegetation implies that these organizing forces reach their highest expression in the association. The association is the most highly individualized vegetational entity."

Organization, interaction, interdependence then represent, according to Tansley, the essential elements in the concept of the plant association. We shall pass, for the moment, the supplementary criteria of maturity and stability, to which we may later have occasion to return.

Entirely different is the picture painted by H. A. Gleason (28). He admits as well founded "the numerous conclusions in synecology which depend directly upon observation or experiment. * * * But our various theories on the fundamental nature, definition and classification of associations extend largely beyond the bounds of experiment and observation and represent merely abstract extrapolations of the ecologist's mind." Here we see, without doubt, the cause of the "apparently chronic inability" of the ecologists "to come to any general agreement on these matters." Nevertheless, "plant associations exist, we can walk over them, we can measure their extent, we can describe their structure in terms of their component species, we can correlate them with their environment, we can frequently discover their past history and make inferences about their future."

All methods which enable us to deepen our objective knowledge of associations are equally to be recommended, says Gleason. But not one of them gives us a solid foundation on which we may build a definition of an association: uniformity in the floristic composition of the vegetation is only an approximation, the correlation between environment and the association is marred by many irregularities, etc. Critical examination thus reveals to us the limited applicability, the doubtful exactness of all the characters generally employed in the definition and classification of plant communities.

In view of this total bankruptcy of facts, "are we not justified in coming to the general conclusion * * that an association is not an organism, scarcely even a vegetational unit, but merely a coincidence?"

Starting from the undeniable principle that "the phenomena of vegetation depend completely on the phenomena of the indi-

vidual,"[10] Gleason proposes to establish "the individualistic concept of the development of plant communities" as the only basis for the concept of the association. Any plant is capable of migrating in any direction by means of its seeds, provided that it meets with favorable environmental conditions. "Every species of plant is a law unto itself, the distribution of which depends upon its individual peculiarities of migration and environmental requirements. * * * It grows in company with any other species of similar environmental requirements, irrespective of their normal associational affiliations. The behavior of the plant offers in itself no reason at all for the segregation of plant communities. In any general region there is a large flora and it has furnished migrating seeds for all parts of the region alike. Every environment has therefore had, in general, similar material of species for the sorting process. * * * Since essentially the same environments are repeated in the same region, their selective action upon the plant immigrants leads to an essentially similar flora in each. The primary causes, migration and environmental selection, operate independently on each flora * * and have no relation to the process on any other area. * * * The effect of these primary causes * * is to determine the plant life on every minimum area. The recurrence of a similar juxtaposition over tracts of measurable extent * * is due to a similarity in the contributing causes over the whole area involved."

"These conditions produce the well known phenomena of plant associations of recognizable extent and their repetition with great fidelity in many areas of the same region."

"Plant associations * * depend solely on the coincidence of environmental selection and migration over an area of recognizable extent and usually for a time of considerable duration. * * * Similar conditions obtain for the development of vegetation in a new habitat." In general, chance plays a considerable part as well in the colonization of a new habitat as in the similarity of populations of "two areas of the earth's surface."

"Under the individualistic concept," and contrary to current opinions, in regard to associations, "the fundamental idea is neither extent, unit character, permanence, nor definiteness of structure.

[10] Starting from a similar principle, Ramenski (60, 61) concludes that associations do not exist and that their study is useless.

It is rather the visible expression, through the juxtaposition of individuals, of the same or different species and either with or without mutual influence, of the result of causes in continuous operation."

So Tansley says *organizing forces, competition, maturity, quasi-organisms,* while Gleason says *chance, migration, environmental selection, juxtaposition.*

Is it not possible that this complete antagonism suggests that both Tansley and Gleason have "forced their conclusions a bit too far?" Both of them probably have good reasons for the evidence which they use, but the conclusions which they draw are not so certain.

The question presents itself from a different angle to us of central Europe and we believe that it may be possible to bridge the chasm which separates the two concepts.

In its general form, the concept of the association implies the coexistence of a certain number of distinct species, living in common, occupying together a piece of habitable environment of large or small extent. Such a cohabitation, capable of almost identical repetition even at distant points of a considerable region, can not be the product of chance alone.

The most meticulous analysis, however, has not been able to demonstrate any evidence of altruism in plant societies. When one speaks of interdependence of organisms within such groups there is no thought of harmonious functioning or of a coöperation of diverse tendencies toward a common end for the collective welfare, as in civilized human societies. Each one for himself; that is the natural law in plant sociology. Each species finds itself there because of natural causes (migration and environmental selection) which permit it to be there, and each one maintains itself there because none of its neighbors is able to dislodge or suppress it. Each species, in general, is dependent on the other species only to the extent that it takes advantage of or profits by the environmental conditions which are determined by the presence of the others.

The term plant association, then, connotes a juxtaposition of specific elements which are strangers to each other and whose coexistence depends on their specific requirements, which may be

satisfied either by the conditions of the environment itself or by those conditions as modified by the presence of the other plants.[11]

Then if one association is succeeded by a second, it is not because one organism (Clements) or even one quasi-organism (Tansley) replaces the other. It is because certain species which have now become more privileged for one reason or another expel or destroy the original occupants; the displacement of the leaders reacts more or less fatally on their satellites (27). Reciprocally, it is certain that a definite, fully stabilized association, more or less in equilibrium with its environment, can never be established at once and *en bloc,* with all its floristic cortege. Like every natural phenomenon which is subject to the same law of evolution, the present state of a plant association, at any moment whatever, is only one stage, more or less advanced, in an ontogeny in which a whole series of individuals can participate.

Tansley scarcely speaks about anything except the reaction of the species on the environment. In our opinion, this is no more sufficient than is the simple elimination exercised by "environmental selection" according to Gleason. As a matter of fact, every species, no matter how modest or transient it may be, is not entirely without some power, we think, of reacting by its presence on the group of plants to which it belongs. This reaction on the whole assemblage must naturally be very variable in nature and intensity, but through it the society can find, in the course of its floristic development, a more or less efficacious, direct or indirect cause of consolidation and stabilization, just as it also finds a more or less menacing danger of disturbance and destruction. In short, every species is, we believe, a biological factor in the society of which it is a part.

In order to establish these ideas, I undertook in 1919 to draw attention to some of the factors in this sociological activity, distinguishing them as constructive, conservative, and destructive. These have since become familiar to a considerable number of European phytosociologists under the name of the dynamogenetic behavior of the species.

[11] Notwithstanding a statement which sometimes slips from the pen of even the most learned, a plant association is not a juxtaposition or cohabitation of organisms with the same demands upon the environment (i.e., the same ecology).

Dynamogenetic behavior is the direct or indirect reaction of the species simultaneously on the composition, the prosperity, and the internal organization of the plant society. In this domain it is probably the most important cog in the social machine. Research into the behavior of each of the specific elements and into their reciprocal reactions injects the dynamic principle into the very heart of the association-concept and thus demonstrates for this fundamental sociological unit the enlivening penetration of the Anglo-American method into the old static discipline of central Europe. We also remark in passing that the determination of the dynamogenetic behavior of species and societies results in placing autecology at the service of synecology.[12]

In conclusion, migration, environmental selection, and dynamogenetic behavior are the three bases which permit us not only to understand the genesis of associations, but also to comprehend and appreciate the differences which distinguish them from accidental and heterogeneous populations and from chance, unstable, and ephemeral juxtapositions. Thus the species depends on the population and the population depends on the species. Stability and equilibrium, realities which are the very essence of a plant society, imply a certain degree of interdependence and natural cohesion; these represent a bond of elementary solidarity which may legitimately be considered, we believe, as a particular type of organization.

Finally, from a philosophical viewpoint, the definite groups of which the association is the essential type appear to us to be stabilized combinations, endowed with a certain degree of permanence within their environment, but in their origin, their continued existence, and their ultimate natural disappearance subject to that universal principle of competition which prevails in all organic evolution, the struggle for existence.

Abstract or concrete?

It appears certain that we can use for the association a language analogous to that used for the species, considering the latter as the fundamental unit in taxonomy. Such, in our opinion, is the philosophical basis for the comparison, made so often and from

[12] The so-called new trend of phytosociology, discerned (?) by Gams (26), implicitly followed (?) by Lippmaa (38), and discovered (?) by Katz (35), does not represent anything new.

such diverse viewpoints, between the association and the species. For example, various analogies have been invoked by Nichols in his interesting paper (43) devoted to a criticism of the individualistic concept of Gleason. And as Du Rietz remarked (15), the analogy between species and associations has often been used and misused during recent years.

It seems that this correlation was first used by Schröter for a purely didactic purpose. The hierarchal subordination of the species to the genus suggested to him a similar subordination of the association to the formation, considered as a superior ecological unit.

According to Tansley (69), "it is impossible to define the concept of the plant association, just as it is impossible to define the concept of a species." We are absolutely of the same opinion, but we must recall briefly some of the secondary questions which have been raised in the controversy concerning the analogies between species and associations.

From the taxonomic point of view, the species is regarded as an abstraction by the great majority of scientists.[13] Does the same hold true for the association?

This question has been asked directly by Alechin (1) and answered by him in the negative through a logic which seems to put all of us more or less in the wrong. This applies particularly to Du Rietz, whose fluctuating opinion, according to his own confession, was scarcely formulated before 1925 (Cf. Du Rietz, 17), and who has definitely declared himself for the exclusively concrete character and for the aggregate concept of the association in the sense of Nichols (42).

On the other hand, according to the most recent American contributions, the *stand* of Christopherson (11), of Nichols (44) and of Gleason (31) becomes the exact equivalent of the *Bestand* or *Einzelbestand* of the ecologists of the Braun-Blanquet school. "We consider every normally developed separate appearance of a definite association as an association-individual (local stand)," wrote Braun-Blanquet in 1921 (5).

The major importance of the stand as the concrete exemplification of the abstract association became clearly evident when Braun-

[13] For the contrary opinion, see Du Rietz (19). But when we say 'the tiger is cruel,' we are speaking in the abstract, and questionable logic can not change it.

Blanquet specified in 1921 (5) that each *Einzelbestand,* each individual of the association, could be used but once in the statistical determination of constancy. Kylin (37) devoted a dozen pages to the defense of the *association-individual,* the existence of which was to him the only reason for the distinction between frequency and constancy. According to Nordhagen (45) this idea is the absolutely indispensable basis for statistics of vegetation, since it concerns natural objects which are especially appropriate for the study of dispersion, homogeneity, and similar features.

Realizing that, according to the very exact definition of Braun-Blanquet, to deny the existence of individuals of an association is to deny the existence of the Bestände or stands, it appears to us useless to refuse such argument. We may merely recall that for Du Rietz himself (17) the idea of the individual of the association is considered a necessity for the partisans of the abstract association.

Then what remains to encourage polemics?

There remain all the pretexts of logic (?), all the linguistic chicanery introduced by Du Rietz (14) and continued with unflagging zeal against the term, against the expression, association-individual.

"Small pieces of any association have been termed 'individuals of the association,' a rather unhappy procedure and one now seldom used," wrote Lippmaa (39), who added, a few pages later, "We have seen that the idea of the individual of the association can not be maintained." The first phrase concerns a term, the second one an idea; these are by no means the same thing!

Lippmaa does not seem to have grasped exactly the thought of Vierhapper (75), who based his opposition on the literal interpretation of the term individual, an opposition therefore purely linguistic. In the ordinary anthropocentric language, this term evidently connotes a sort of constitutional unity, as realized for example in the body of a vertebrate, the dismemberment of which would lead to the actual loss of the individual personality.

Even Lüdi (41), one of the most brilliant representatives of the Zürich school, allowed himself to be influenced by the argument of Vierhapper. Although a firm defender of the *Bestand,* he condemned the term association-individual "not for reasons of logic, but because the term 'individual' awakens too easily the

impression of an indivisible thing, corresponding to an individual living thing."

When I proposed in 1912 (48) the term *individu d'association* (originated at the suggestion of Schröter in 1902), I had no other object than to enable the field ecologist to express his results in the French language as logically as the taxonomist expresses the results of his field study. The same argument was used later by Kylin (37) in favor of the *Bestand,* and Nichols (43) wrote at the same time "As will be apparent presently, the *stand* holds very much the same relation to the association * * that the individual plant, in the field of taxonomic botany, holds to the species."

In other words, and with philosophical reservation that "any comparison between the association and the species is purely in the nature of an analogy" (Nichols, 43), we may admit that the plant association, an abstract unit like the species, is represented, again like the species, by individuals (*individus d'association, Bestände, stands*), large or small in area and more or less scattered over the surface of the earth.

Diagnosis of associations

All those who during the past thirty-five years have followed the development of plant ecology can not have forgotten the deep impression created by the publication of Schröter's memoir "Vorschläge für eine Nomenklatur der Formationslehre," included in the botanical section of the Monographie du lac Constance (68). Under Schröter's vigorous impulse, synecology has impressed itself on the science of central Europe as a collective term, embracing all phases of the study of vegetation. It was his synecological concept, embodied in the definition of the plant association to which we have referred in the first lines of this article, which was presented, without much success, to be sure, to the consideration of the section of phytogeography at the Congress of Brussels in 1910.

There is one feature in this definition which has persisted since the beginning of the century and which has never ceased to hold good under the most diverse conditions: *the association should be characterized by its floristic elements.* One can even say that the search for the floristic solution of the problems of vegetation, regarded as groups of plants, is in some respects the very object of plant sociology.

The first solution which led to some fertile results is that of Brockmann-Jerosch (10), for it is he who for the first time advocated and practised the method of segregating the species of a vegetational group into three categories, the constants, the accessories, and the accidentals. He thus utilized a statistical selection with results which serve far better to characterize a group than a simple list of species. Only the methodical use of such principles of subordination appears to us to be capable of directing the search toward criteria which are truly indicative of and in conformity with the natural conditions and with the interdependence of the species; capable, in a word, of yielding essential and indispensable criteria for the rational diagnosis of plant associations.

Such, in our opinion, was also the chief value of the method introduced and gradually developed by Braun-Blanquet from 1913 to 1918. This places the chief stress on fidelity, a sociological idea, rather than on dominance or constancy, which are purely plastic or demographic ideas in the sense of Harper (33). It first attracted attention under the name of the floristic method, which Braun-Blanquet himself had given it, but it better deserved from the outset the name floristic-ecological method. Indeed, prejudice, as persistent as it is inaccurate, has often given it a strictly systematic character. But it appears from the words of Braun-Blanquet himself (3) that, although the method is based solely on floristic composition, it requires none the less an appreciation of the importance of the relation of the species to each other and to their environment which in itself is the only justification for separating these elements.

Then appear Du Rietz and his colleagues (22), whose laws maintain that all the past must be swept away in favor of the Upsala technique, which alone is wholly accurate and trustworthy. We have already mentioned the present attitude of Du Rietz toward this method of work, the abandonment of which—we might almost say the condemnation—coincides with a radical change in the style of his descriptions. The initiative of the Upsalians has nevertheless had an undeniable influence on the development of our science in continental Europe.

Before proceeding with the analysis, it is interesting to note the almost total lack of any noticeable reaction on the Anglo-American

scientific mentality. Since then as well as before, the great majority of ecologists of the English language have remained serenely faithful to the idea of dominants, in the sense of Clements, Tansley, and Nichols,[14] as the necessary and sufficient factors in the recognition, naming, and description of associations. Far from being misled or diverted by European trifles, they have continued to advance with admirable discipline along the path blazed by Cowles and by Clements, their eyes fixed on the splendid goal of positive knowledge and philosophical divination where shine, in letters of gold, the three magical words *succession, development, change*.[15]

Before closing these parenthetical remarks, it may be useful to recall that Du Rietz in 1930 (18), in his characterization of the sociation and other units in his system, gave a major rôle to dominants, which he defined as follows: "A dominant is a species which, either alone or together with one or several other species of about the same size, constitutes the bulk of the vegetation of its layer." The idea of stratification, more or less secondary in the definition of Tansley and Chipp, here assumes the rôle of a decisive systematic factor.

One is not surprised to find echoes of this idea in the most recent work of Katz (35) and of Lippmaa (40), but differing from each other in every respect.

Even more radical than Du Rietz himself, Katz claims that associations should be characterized only by the dominant species in each layer of the society. He defines a dominant species as "one which has the greatest dominance or the highest coverage in the association" (35). Floristic composition and stability, as well as physiognomy and site, should be eliminated, as useless or misleading, from the diagnosis of the association, which Katz accepts as the fundamental unit of plant sociology, but only in a very reduced size, corresponding to the sociation of Du Rietz (18).

According to Lippmaa (40), the separation of associations is possible only through the floristic composition as the point of de-

[14] A sense which is essentially physiognomic and plastic: "In all closed vegetation, i.e., where the ground is fully occupied by plants, certain species dominate the community. They are most commonly those which grow tallest and are most numerous in the upper layer or stratum of the vegetation" (73; see also 70, pp. 243, 246). "Certain plants are dominant, in the sense that they determine the physiognomy of the association" (44).

[15] The historical order. The logical order may be *change, succession, development.*

parture, and as practicable only in a stabilized vegetation in equilibrium with its environment. The technique recommended by Lippmaa for the study of associations in the field is that of Braun-Blanquet, but the Esthonian author exalts the importance of stratification more than any of his predecessors. For him each layer corresponds to a distinct association; as many the layers, so many the associations, and these layer-associations are for him the fundamental units of vegetation. In our opinion this process of systematic dismemberment of the association is likely to lead to a pulverization still more excessive than that of Du Rietz and Katz.[16]

But to return to our subject.

The idea of letting minimum area and minimum number of species play a part in the recognition of plant association was first formulated by Braun-Blanquet (2), whose most recent statement reads "A community of plants requires for its normal development a minimum area and also upon this area a minimum number of plant species." This idea of a similar relation between an area (minimum area) and a group of species qualitatively defined (the constants) as a necessary requirement for the diagnosis or definition of the association first appeared in the didactic memoir of Du Rietz and his colleagues in 1920 (22). Since that time the most striking result of their activity is that they have imposed on all of us the necessity of including statistical research in our general analyses of plant associations, thereby adding the quadrat method and the graphic expression of its results to the construction of a really accurate description.

Now the smallest amount of space which can be truly characteristic of a society is one which has a single individual of the rarest species, together with a mass of individuals of all other species of the society, the relative number and distance of the individuals of each species being determined by their respective density in the society. In practice, the size of the minimum area can be read directly from a graph showing the relation of species to area, or from the *species number : area* curve, reading the area as the abscissa of the point where the curve tends to approximate a straight line. In order to secure maximum accuracy in this com-

[16] Lippmaa foresees (40) that it will be necessary to distinguish two or three associations in a single "synusia of the second degree," in the sense of Gams (24).

putation, Lippmaa recommends that all accidental species should be neglected.

The actual number of species in this minimum area is in itself of only secondary interest. The essential value of its species, according to Braun-Blanquet (6), is that they represent a characteristic combination (an expression of E. Schmid, 67), comprising a limited number of species which appear in the area because of their high coefficients of fidelity and presence.

The importance of species of a high degree of presence is evident from the quantitative point of view, since the dominant species belong in this group. As to the characteristic species, in the sense of Braun-Blanquet, belonging to the three highest classes of fidelity, their qualitative importance is still greater from a sociological viewpoint, since they are often indicators of the ecology, development, or classification of the society.

Another stage was thus reached, whose opportuneness has stood the test of time.

But a beautiful, although essentially static, concept of the association was no longer sufficient against the irresistible wave of opinion which, originating in America, had already captured the British thought and aroused a lively interest in the dynamic and genetic viewpoint in several scientific centers of continental Europe.

On the other hand, the thorough study of the soil was brought into the lime-light at the same time through the results of research in biological applications of physical chemistry (46, 64, etc.) and in the genesis of soils by Glinka (32) and other Russian pedologists. As Pallmann and Haffner (47) justly say, "Soil, climate and vegetation form a solid *unit*. The properties of the soil are reflected in the characteristics of the vegetation which it produces, and that in turn reacts strongly on the formation of soil, while climate gives special features to both of them. Research in plant sociology is scarcely to be considered today unless it takes into account the environmental conditions of soil and climate." And Tansley writes: "The more detailed elucidation of the relation of soil evolution to the development of vegetation is the most important co-operative task of the immediate future for pedologists and ecologists."

To this program, which is now before us, several anticipatory answers have already been given during the past ten years. We

would particularly call attention to that of Braun-Blanquet and Jenny (9), based upon study of the alpine meadows in the Swiss National Park, since it deals especially with the parallelism between soil evolution and vegetational development and since it demonstrates in a general way the course of this double evolution over a large part of central Europe.

"In a work carried out in cooperation with a soil chemist (H. Jenny), we insisted, in 1926, on the fact that there exists a close and reciprocal relation between the natural development of the vegetation and the evolution of the soil. This relation, controlled primarily by the general climate of the region, discloses for central and northwestern Europe a progressive acidification of the soil, continuing to the final stage of soil maturity. Parallel with this acidification, the pioneer basiphile or weakly acidophile societies are succeeded by increasingly acidophile associations. The terminal stage, to which the succession tends, is purely acidophile. This evolution is not reversible; it may be considered a natural law.

"To the great climatic soil provinces (pedoclimax) there correspond climatic climaxes of vegetation." (Braun-Blanquet, 7.)

In other words, this evolutionary synthesis leads to the more significant idea, the vegetational climax on the mature soil, a symbol of perfect equilibrium and a criterion of stability, if not of permanence, as long as the present climate endures. If climatic climaxes were reached over the whole world, universal stability would result; this is not the case for many reasons. If it is true that "every association represents a more or less stable and enduring stage in the successional series" (Lüdi, 41), then the general characteristic of the present world is, in the brilliant phrase of Cooper (13), "the universality of change."

Summary

1. The association as defined by Braun-Blanquet is the fundamental unit of plant sociology.

2. The plant association is an abstract unit, represented in nature by *individus d'association, Bestände, stands,* large or small, and more or less scattered over the surface of the earth.

3. There is a close reciprocal relation between the natural evolution of vegetation and the evolution of the soil. This evolution,

controlled primarily by the general climate, leads finally to the vegetational climax on mature soil. Before that stage, each association represents a stage of fluctuating stability and duration.

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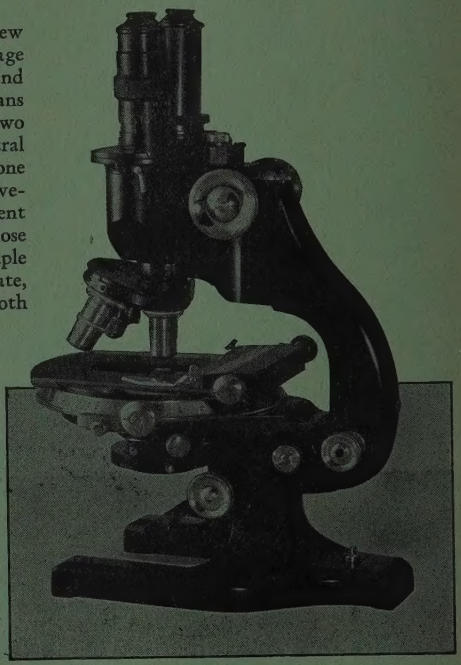

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